Stage- and weather-dependent dispersal in the brown garden snail Cornu aspersum

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Abstract

Dispersal decisions are often condition-dependent, influenced by the interaction of individual phenotype and environmental conditions. Terrestrial Gastropods are simultaneous hermaphrodites, a reproductive system rarely studied in the context of dispersal. Moreover, the energetic cost of their movement is one of the highest among animals. Despite these features, which make them valuable models to understand the trade-offs between dispersal and other life-history traits, their dispersal strategies have been barely explored. We studied the movements of subadults and adults of the brown garden snail *Cornu aspersum* in a semi-natural 4-patch network, for two months in 2011 (a dry year) and one month in 2012 (a wet year). We assessed the effects of life-history stage (subadult/adult) and weather conditions on dispersal propensity and dispersal speed. Snails were more mobile under humid and warm weather, but nearly all individuals left patches when the relative humidity was close to 100 % in 2012. Because such humidity levels are potentially lethal to *C. aspersum*, we argue these extreme emigration rates might be an emergency escape response to harmful conditions. Despite a theoretically higher cost of movement, we found that subadults emigrated more, and dispersed faster and further, than adults. Thus, and contrary to what was expected, direct costs of movement do not play the main role in shaping dispersal in *C. aspersum*. Observed differences between subadults and adults in dispersal behaviour are discussed in the context of intraspecific competition, inbreeding avoidance and relative costs of male and female reproduction.

Keywords Dispersal distances · *Helix aspersa* · Life-history strategies · Natal dispersal · Phenotype-dependent dispersal

Introduction

Dispersal, defined as "any movement of individuals or propagules with potential consequences for gene flow across space" (Ronce 2007), plays a key role in many ecological and evolutionary processes (Bowler and Benton 2005; Clobert et al. 2012). Benefits of dispersal include reduced kin competition, inbreeding avoidance, and coping with environmental stochasticity (Starrfelt and Kokko 2012). It is now widely acknowledged that dispersal is not a species-fixed trait, but can be highly variable both within and among populations (Clobert et al. 2012). One reason is that benefits and costs of dispersal vary across environments, between sexes and between different age classes, leading to context-, sex- or age-related differences in dispersal propensity and dispersal distances (Bowler and Benton 2005; Bitume et al. 2013). Moreover, the effect of environmental conditions is likely to differ between sexes or life-history stages, leading to potentially complex interactions (Bowler and Benton 2009). These aspects have been mostly studied in arthropods, vertebrates, and plants, leading to a strong taxonomic bias in our understanding of dispersal. Thus, consistent information about dispersal is still lacking for a wide part of the range of existing life histories, including some otherwise well-studied groups.

Land snails and slugs (Stylommatophoran gastropods) form a highly diverse group of molluscs, with more than 30,000 species distributed all around the world in a great variety of ecosystems (Barker 2001a). Many species are important crop pests in and outside their native range (Barker 2002), and some introduced species have colonized natural habitats, with negative impacts on native biodiversity (Cowie 2011). Thus, knowledge of their dispersal capacities is of conservation and economic interest (Aubry et al. 2006; Honek and Martinkova 2011). In terrestrial gastropods, long-distance dispersal and introductions across regions are passive processes, mainly mediated by wind, water and human transport (Dörge et al. 1999; Aubry et al. 2006). However, expansion and gene flow at local scales seem to depend mostly on active dispersal (Aubry et al. 2006). Despite that, to date, studies of the active movement capacity of land snails and slugs are rare, and mainly descriptive (see Baur 1993a, 1993b; or Aubry et al.

2006, for notable exceptions). We nonetheless believe that a better understanding of dispersal in land snails and slugs can shed new light on some general questions about the ecology and evolution of dispersal. Indeed, their peculiar life histories may have led to original, yet unstudied, dispersal strategies.

Stylommatophoran gastropods are simultaneous hermaphrodites, with a tendency for protandry in at least some lineages (Barker 2001b). The presence of both male and female reproductive organs in a single individual adds a dimension to dispersal/reproduction trade-offs, which play a key role in the evolution of dispersal (Ims and Hjermann 2001; Danchin and Cam 2002). In gonochoric animals, sex-biased dispersal can be selected as a means to avoid inbreeding, by increasing the distance between opposite-sex siblings (Perrin and Goudet 2001; Costello et al. 2008). Sex-biased dispersal can have profound effects on metapopulation dynamics, for instance by altering the speed of colonisation processes (Miller and Inouye 2013). It can also increase the extinction probability of small populations, by increasing the mismatch between the male and female spatial distributions, thus decreasing the chances to find a mate for both the dispersing and the philopatric sex (Dale 2001; Miller and Inouye 2013). Under similar selective pressures, we can expect that hermaphroditic animals would evolve quite different dispersal solutions, with potentially different consequences on population dynamics.

Costs of dispersal have been repeatedly shown to be instrumental in the evolution of this behaviour (Bonte et al. 2012). Costs are of different types (e.g., energetic, mortality or time costs) and can be incurred at all stages of the dispersal process (before emigration, at departure, during transience, and at settlement). These costs usually lead to trade-offs between dispersal and other life-history traits. For instance, in winged insects, increased resource allocation to wings and muscles is typically done at the expense of fecundity (Guerra 2011). Moreover, actively dispersing individuals are expected to adjust their decisions to settle or continue based on currently perceived costs, affecting the distribution of dispersal distances (Bonte et al. 2012; Bitume et al. 2013). The energetic cost of movement in snails and slugs is one of the highest

among animals; they spend about 10 times more energy per meter moved than any other terrestrial animal of similar weight (Denny 1980). Moreover, because of their relative slowness, dispersing snails and slugs might be subject to a higher predation risk compared to more mobile animals, increasing the mortality cost of dispersal. However, land snails also carry a protective shell of variable thickness, which limits predation by non-specialists (Barker 2004), as well as decreases the risks associated with body water evaporation under unfavourable conditions (Klein-Rollais 1993). These characteristics make this taxon an interesting model to understand how dispersal costs, in particular costs during transience, interact with each other and affect the trade-offs between dispersal and other life-history traits.

Here we investigate the potential changes in dispersal capacity between life-history stages in the brown garden snail *Cornu aspersum* (Müller) (fam. Helicidae; syn. *Helix aspersa* Müller). Native of the Mediterranean area, this relatively large land snail (shell diameter at maturity: 25 to 40 mm) has been spread throughout the world by humans, either voluntarily, for food purposes, or accidentally (Guiller et al. 2012). This species is now considered invasive and is an agricultural pest in many regions outside its native range (Barker 2002; Guiller et al. 2012). Despite being one of the most studied land snail species (see references in Barker 2001b), there is no available information about its active dispersal in the literature. However, in *C. aspersum* and some related species, the level of locomotor activity has been shown to vary between life-history stages (Oosterhoff 1977; Fearnley 1993). Even though dispersal was not measured in these studies, they suggest the existence of stage-dependent dispersal in helicid land snails. In this context, we studied how the first two phases of dispersal (i.e., departure and transience) differed between subadults and adults of *C. aspersum*, using individually marked snails in a closed semi-natural system. As snail activity is highly weather-dependent (Bailey 1975), we included rainfall, temperature and humidity as covariates in our analyses. Because of the high energetic cost of movement in terrestrial molluscs (Denny 1980), we expected adults to disperse more frequently and/or faster and further. Indeed, when dispersal is particularly costly, larger

individuals are more likely to disperse, because they have the energy reserves to cope with these costs, and because they are more likely to successfully immigrate in a new, competitive patch (Bowler and Benton 2005).

Material and Methods

Collecting and maintenance of snails

All individuals were collected at the end of the hibernation season (March 2011 and April 2012) in wild populations from north-western France. Only individuals whose shell diameter was higher than 22 mm (i.e., stage II juveniles and adults, Klein-Rollais 1993) were used. Individuals which had ended their somatic growth ("adults") were distinguished from stage II juveniles (hereafter named "subadults") by the presence of a reflected lip around the shell aperture (Klein-Rollais 1993). Subadults were on average smaller than adults ($F_{1,658} = 440.8$, $P < 0.001$; mean shell diameter ± standard error in subadults: 26.5 ± 0.2 mm, $n_{2011+2012} = 329$; in adults: 30.4 ± 0.1 mm, $n_{2011+2012} = 331$). Snails were kept in controlled conditions (20 °C, 80 % R.H., 16L 8D photoperiod) for at least two weeks before release. They were housed in polythene boxes (30 × 45 × 8 cm) covered with a plastic mesh (30 individuals per box). To provide a moist substrate and a source of water for the snails, the bottom of each box was lined with synthetic foam kept saturated in water. Snails were fed *ad libitum* with a composite snail food (cereal powder supplemented with calcium; Ets Berton, France).

Monitoring of snail dispersal in semi-natural conditions

To study the effect of life-history stage and weather on dispersal movements, an experimental network was built in a meadow, on the Beaulieu university campus, Rennes (Brittany, France; 01°38'05" W, 48°06'51" N). This 13 x 50 m network included four 9 m² square patches of vegetation connected by four corridors, fenced with 15 cm high concrete block walls (Fig. 1). To limit snail evasion and bird predation, the network was covered by mesh (mesh size: 18 mm in 2011, 12 mm in 2012). Two corridors were 1.2 m wide, while the others were 0.8 m wide.

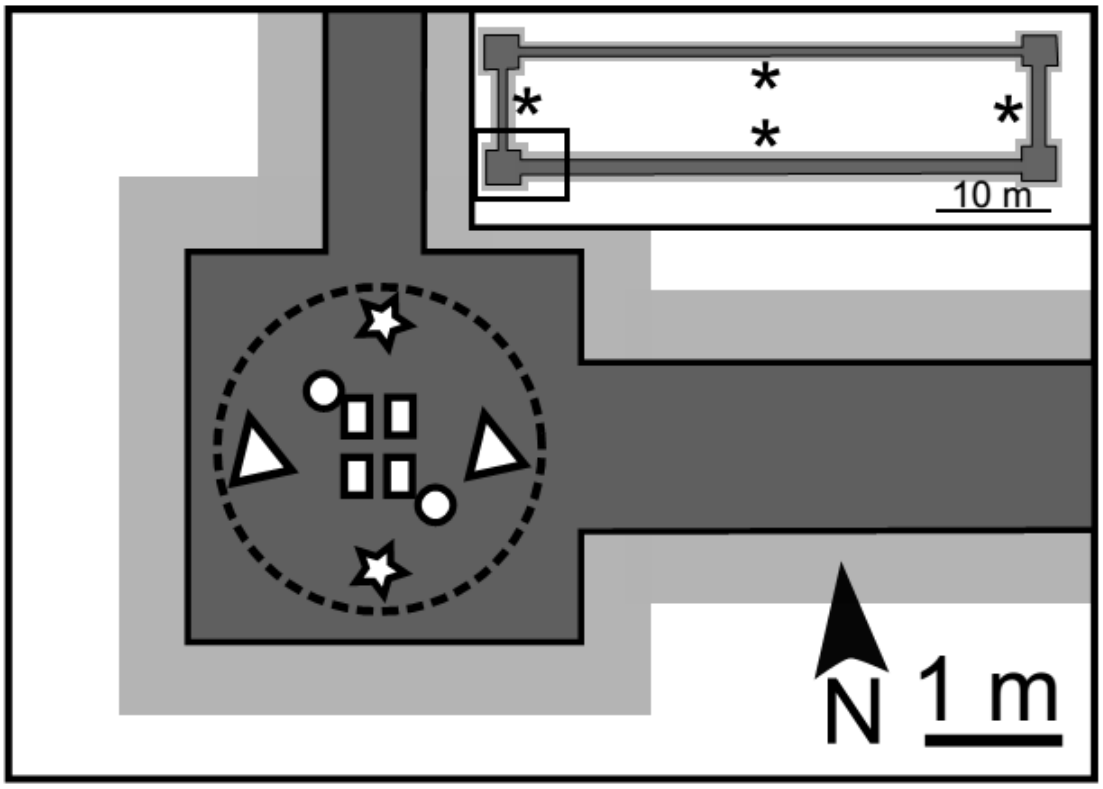

Figure 1 Schematic representation of a patch in the experimental network (dark grey), showing the disposition of corridors and the buffer zone (light grey) where any individual found was put back in the network. The resources available to snails inside patches are also represented: rectangles = shelters; triangles = nettle spots; stars = ivy spots; circles = composite snail food in plastic plates (in 2011 only). The dotted circle marks the limit beyond which snails were considered dispersers. Inset: a representation of the entire network. The asterisks mark the location of the climatic probes.

The ground was homogeneously covered by red fescue (*Festuca rubra* L.) and perennial ryegrass (*Lolium perenne* L.), and was gridded to ease the recording of snail coordinates. Wood and brick shelters were placed in each patch, big enough to shelter about 150 individuals per patch. Nettle (*Urtica dioica* L.) and ivy (*Hedera helix* L.) spots were planted (2 spots of each species per patch). Nettle leaves are particularly palatable to *C. aspersum* (Iglesias and Castillejo 1999) and ivy is one of its main host plants in the wild (Stratton 1964). In 2011, drought impeded nettle and ivy growth, requiring the supplementation of food resources for this year; thus, 100 g of composite snail food per patch were added in plastic plates near the shelters. Two climatic probes (Log32 datalogger, Dostmann, Reicholzheim, Germany) were installed at

the western and eastern extremities of the network to record ground-level temperature and relative humidity at hourly intervals. As snails started to use northern and southern corridors in 2012, two supplementary probes were installed near the middle of these corridors (Fig. 1). Daily rainfall data were obtained from the Météo-France station of Rennes-St Jacques.

On 1st April 2011, 300 snails were released in the network. They were divided into four groups: two composed of 50 individuals (in the north-eastern and the south-western patches) and two composed of 100 individuals (in the north-western and the south-eastern patches). We initially chose different group sizes to determine if density affected dispersal. No significant effect of these density levels on dispersal metrics in 2011 was found (Generalized Linear Mixed Model with the emigration rate as a response variable and with weather and life-history stage as covariates, $z = -0.223$, $P = 0.82$). Thus, this distinction was abandoned for the 2012 session and the density effect not included in the complete analyses. After monitoring, the network was cleared of all remaining snails. On 4th June 2012, 360 new snails were released, divided into four equal groups of 90 individuals. To avoid an increase of dispersal due to translocation stress (Turchin 1998), release took place during the inactivity period (day), and snails were placed in or at the immediate proximity of the shelters. One hour after release, only a few individuals were outside the shelters (between 1 and 3, depending of the patch). Each released snail was marked with two numbered and coloured plastic marks commonly used for honeybees, glued with cyanoacrylate (Henry and Jarne 2007). Adults and subadults were in equal numbers in each population. Bonferroni-corrected Kolmogorov-Smirnov tests were used to ensure that shell size distributions of adults and subadults did not differ significantly between populations and between years. Individual locations were recorded twice a week for 52 days in 2011 and 25 days in 2012, with a week of interruption in 2012. Monitoring was prematurely interrupted in 2012 because of a high escape rate (see Results for a possible explanation): based on a Cormack-Jolly-Seber model with lost individuals considered “dead”, only 36.1 % of the released individuals in 2012 were still in the network after 25 days in 2012 (130 snails of 360; 95 %

confidence interval: 100 – 168) against 73.0 % after 52 days in 2011 (219 snails of 300; 95 % CI: 208 – 231). Snails were searched for in the experimental network itself and in a 50 cm wide buffer zone around it (Fig. 1). When a marked snail was found in the buffer zone, it was placed, after its coordinates were noted, at the nearest point inside the experimental network.

Statistical analyses

All statistical analyses were carried out using R (version 2.14; R Development Core Team 2011).

In this study, we considered as "resident" any snail found inside a circle of radius 1.20 m including its original shelter, nettle and ivy spots (Fig. 1). Indeed, *C. aspersum* snails do not usually forage that far when food is available near shelters (Bailey 1989). We assumed that recapture probability of residents was equal to 1. To avoid counting short explorations as dispersal, only snails that were not resident on at least two successive recapture occasions were considered "dispersers". We considered the same patch, observed two consecutive years, as two different patches in analyses.

To study the first step of dispersal, i.e., departure, we analysed the emigration probability between two successive recaptures as a function of life-history stage and weather using Generalized Linear Mixed Models (GLMMs) with the binomial error family and a logit link function. For each patch, emigration was analysed at the group level, as the proportion of individuals of a given life-history stage which dispersed between recaptures. Three weather variables with potential effect on snail activity were considered: mean daily rainfall, mean temperature and mean relative humidity. As the correlation between daily rainfall and mean relative humidity was weak ($R^2 = 0.11$), both variables were conserved in analyses. Because all recaptures were not separated by the same amount of time, we added an effect of interval duration. A year effect (factor with 2 levels) was also added. Finally, to test for differing responses to life-history stage and weather between years, interactions between these variables

and year were added. The patch of origin was included as a random effect, to account for both spatial correlations (between subadults and adults from a same patch) and repeated measures.

To study the second step of dispersal, i.e., transience, we analysed two variables: the maximal dispersal distances observed and individual dispersal speeds. Maximal dispersal distances were analysed using linear models as a function of time since release and year, intercept being forced to zero. Dispersal speed is the speed at which an individual moves away from its original patch, calculated between the last recapture within the release patch and the last recapture as a disperser. Because, under the assumption of (correlated) random walk, the expected linear distance travelled does not increase linearly with time (Turchin 1998), and because dispersal duration differed between individuals, the ratio distance travelled/time is a biased measure of dispersal speed. To correct for this, we calculated for each individual its diffusion coefficient $D = MSD / 4t$ (in m^2/day), where *MSD* is the Mean Squared Displacement, i.e., the mean squared distance between recaptures, and t is the mean time between recaptures (Turchin 1998). Excluding dispersers lost before they could be recaptured, this dataset contained 170 dispersing individuals (74 subadults, 96 adults). The distribution of diffusion coefficients was skewed, so we analysed the effect of weather and life-history stage using Gaussian GLMMs with a log link function. As for emigration, mean daily rainfall, mean temperature and mean relative humidity (at the nearest probe) were included as weather covariates. We considered both the patch of origin and the corridor used to disperse as random effects, to account for spatial correlations. Here, no year effect was included, as most models with such an effect failed to converge.

For both emigration rates and diffusion, a set of models was derived from the full models outlined above. These GLMMs were fitted using the lme4 R package (Bates et al. 2011). This gave a set of 275 possible models for emigration and 16 possible models for diffusion. Selection among these candidate models was realized in an information-theoretic framework, using the Akaike Information Criterion (AIC; Burnham and Anderson 2002). For each set, models were ranked by AIC, the model with the lowest AIC being considered the best and models with ΔAIC

= AIC_{model} - $AIC_{best\ model} \leq 4$ considered "good models". As each set contained more than one "good model", Akaike weights (summing to 1) were calculated and inferences were done by model averaging over the complete set of models (Burnham and Anderson 2002), using the MuMIn R package (Bartoń 2012). Averaging was done with shrinkage (predictors were averaged over all models, with their parameter values set to zero when they are absent from a given model).

Results

Weather differences between the two years (Table 1)

The 2012 session was significantly wetter than the 2011 session: wet days were more frequent in 2012 (χ^2 test, $\chi^2 = 4.84$, $df = 1$, $P = 0.03$), mean daily rainfall was also higher (Mann-Whitney-Wilcoxon two-sample test, $n_{2011} = 52$, $n_{2012} = 25$, $U = 363$, $P < 0.001$), as well as relative humidity (ANOVA, $F_{1,\ 1868} = 254$, $P < 0.001$). Mean temperature, however, was not significantly different between years ($F_{1,\ 1868} = 1.81$, $P = 0.18$).

Table 1: Weather differences between the two field sessions (2011 and 2012).

	2011	2012	*P*
Proportion of wet days (rainfall > 1 mm)	11.5 % (6/52)	40.0 % (10/25)	***
Mean daily rainfall (mm)	0.4 ± 0.2	2.9 ± 1.1	***
Mean relative humidity (%)	70.0 ± 0.7	83.1 ± 0.5	***
Mean temperature (°C)	16.1 ± 0.2	16.5 ± 0.2	> 0.05

Mean values are presented ± SE. Mean values for temperature and humidity are those recorded at the eastern probe. Values from other probes are not significantly different ($P > 0.05$ for all variables). ***: $P < 0.001$; see text for details of tests.

The departure stage: emigration rate between recaptures at the patch level

The cumulated proportion of dispersers increased over time in both years (Fig. 2). In 2012, a proportion higher than 90 % was attained between 2 and 14 days after release and more than 30 % of snails emigrated as soon as the first day post release. In 2011, this 30 % proportion was not attained before 31 days post release.

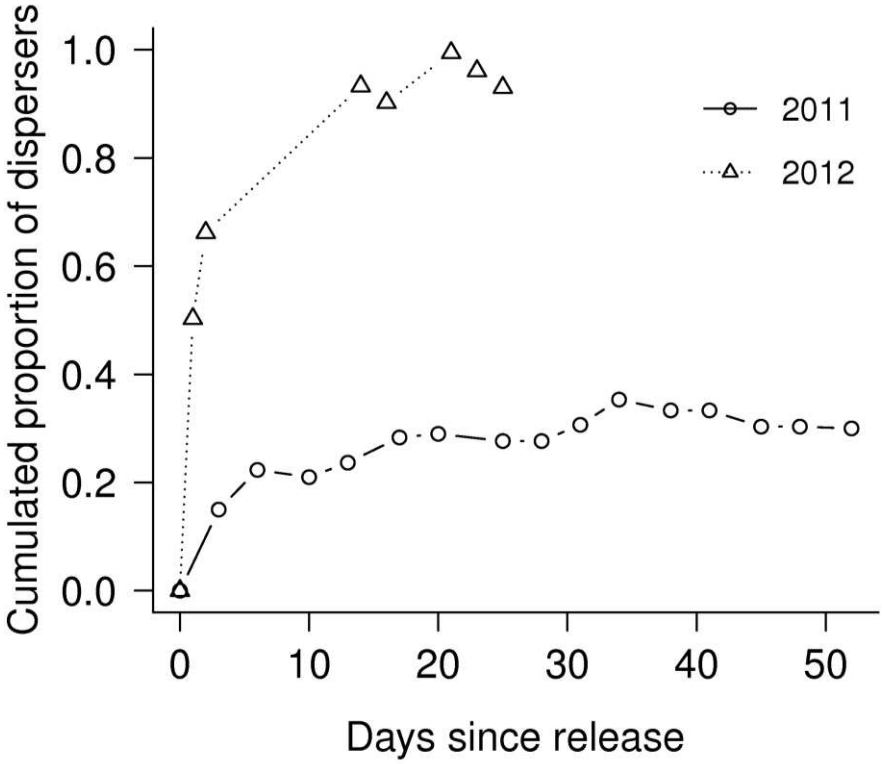

Figure 2: Cumulated proportion of dispersing snails as a function of time since release and year. For each year, data from the 4 patches are pooled; $n_{2011} = 300$, $n_{2012} = 360$.

During the two monitoring sessions, 423 snails (90 in 2011, 333 in 2012) moved more than 1.20 m away from the release point and were considered dispersers. Among these dispersers, 59.8 % (253 of 423 snails) were never recaptured outside the patch, indicating a probable escape from the network as soon as dispersal occurred. Despite numerous precautions to ensure that the network boundaries were as hermetic as possible, snails were several times observed to use small openings (sometimes initially smaller than their shell) to crawl between the mesh and the

soil and/or concrete blocks. Overall, 82.3 % of dispersers (347 of 423 snails, both years combined) escaped from the network during the dispersal process (including both never recaptured snails and individuals lost during dispersal; Fig. S1 in Electronic Supplementary Material (ESM)). This proportion was independent of year and days since release (Fig. S1 in ESM), which would indicate the number of escapees depended only on the number of dispersers, the perimeter/surface ratio of the network, and the number of hidden openings.

Among the 275 models tested for the probability of dispersing between recaptures, 22 were considered "good" ($\Delta AIC \leq 4$; Table S1 in ESM). Thus, inferences on emigration were based on average coefficients, calculated over all models (Table 2). Among the three weather variables, the humidity effect was the only one different from zero, based on 95 % confidence intervals, and the only one to gather substantial support from data (evidence weight = 1, Table 2). Emigration was on average positively correlated with mean humidity levels. There was an interaction between year and humidity: the increase of emigration in response to humidity was stronger in 2012 than in 2011 (Table 2, Fig. 3). Near saturation, the daily emigration rate was much higher than at intermediate levels of humidity (82.3 % of individuals leaving their patch per day of R.H. $\geq$ 90 %) (Fig. 3). Finally, emigration was stage-dependent, with subadults emigrating more than adults (evidence weight = 0.93, Table 2). Using the fact that, in GLMs and GLMMs with a logit link, the parameter value is the logarithm of the odds, we calculated that subadults were on average 1.16 times (exp(0.15)) more likely to emigrate than adults (95 % CI = [1.03; 1.31]).

Table 2: Averaged model parameters for the emigration probability between successive recaptures. Parameter values are averaged over the complete set of models with shrinkage (see Table S1 in ESM).

	Average effect ± SE	Parameter weight
Subadult	0.15 ± 0.06 *	0.93
Interval duration	0.04 ± 0.01 *	1.00
R.H.	0.20 ± 0.03 *	1.00
Year	-22.93 ± 7.51 *	1.00
Year × R.H.	0.31 ± 0.09 *	1.00
(Intercept)	-16.27 ± 3.23 *	1.00
Temp.	-0.07 ± 0.08	0.43
Rain	-0.02 ± 0.09	0.71
Year × Subadult	0.02 ± 0.14	0.23
Year × Interval duration	-0.02 ± 0.02	0.34
Year × Temp.	0.11 ± 0.29	0.12
Year × Rain	-0.23 ± 0.13	0.44

Parameter weight: the sum of the AIC weights of all models in which the parameter appears. Subadult: effect of the life-history stage being "subadult", compared to adults; Interval duration: time between successive recaptures; R.H.: mean relative humidity; Temp.: mean temperature; Rain: mean daily rainfall. Interactions between the year effect and other variables are denoted by a "×" sign. *: average parameter value different from 0, based on 95 % confidence intervals.

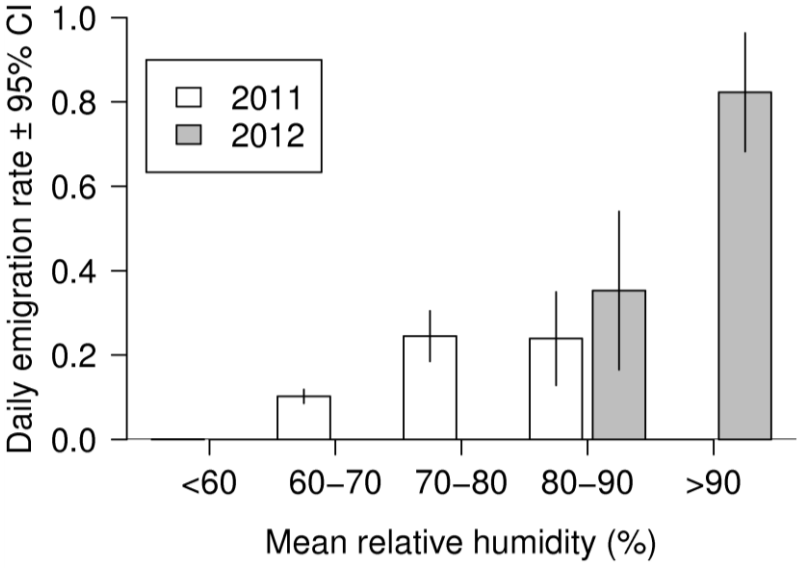

Figure 3: Mean (± 95 % confidence intervals) daily emigration rates observed for five 10 % wide classes of relative humidity, depending of the year. When intervals between recaptures were longer than one day, daily emigration rates were estimated as 1 - (proportion of non-dispersing snails between recaptures) $^{1 / \text{days between recaptures}}$. 95 % confidence intervals are ± 1.96 SE.

The transience stage: maximal dispersal distances

Maximal dispersal distances observed increased with days since release (Fig. 4). This increase was, on average, 9.6 times faster in 2012 than in 2011. Distances of 10 m (i.e., the distance between the centres of two adjacent patches) were attained in 31 days in 2011 and 2 days in 2012. In 2012, the 10 fastest snails travelled the 45 m separating the western and eastern extremities of the network in 23 days, with the fastest observed snail completing the distance in 15 days.

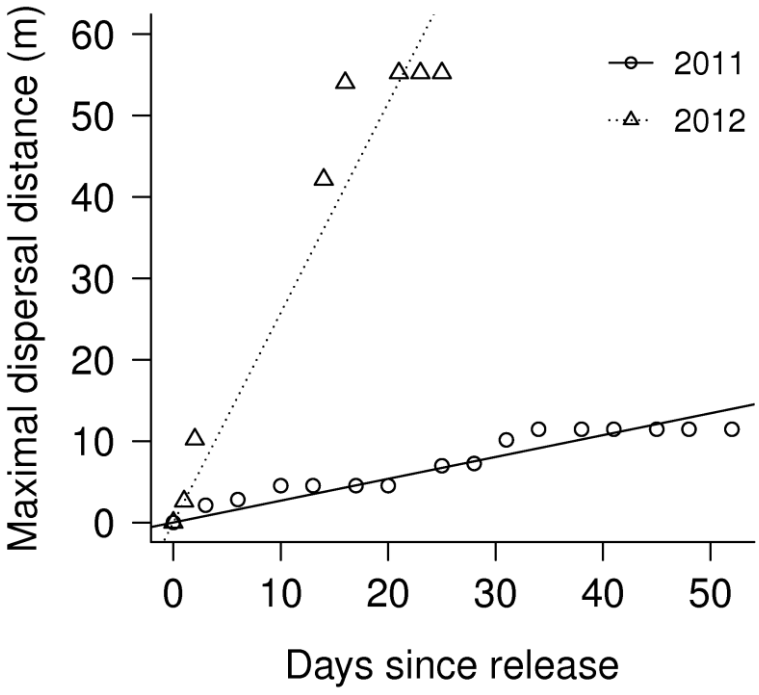

Figure 4: Maximal dispersal distances observed within the experimental network, as a function of year and time since release. Predicted values (lines) are based on a linear model with days as covariate and year as a factor (n = 23, R^2 = 0.97). $y_{2011} = 0.268\,x$, $y_{2012} = 2.576\,x$, the intercept values being set to zero by construction.

The transience stage: individual diffusion coefficients during dispersal

Observed diffusion coefficients ranged between 0.06 and 28.92 m²/day in adults, and between 0.29 and 53.38 m²/day in subadults ($mean_{adults}$ ± SE = 5.84 ± 0.70 m²/day; $mean_{subadults}$ ± SE = 8.84 ± 1.21 m²/day). Among the 16 models analysed, four were considered "good" (ΔAIC ≤ 4; Table S2 in ESM), including the full model. Thus, inferences on diffusion coefficients were based on average coefficients, calculated over all models (Table 3). Dispersal speed was on average positively correlated with all three weather variables: mean rainfall, mean relative humidity and mean temperature between successive recaptures (Table 3). However, the mean rainfall effect was the only one different from zero, based on 95 % confidence intervals (Table 3). Furthermore, the mean rainfall effect was the only one to gather substantial support from data, with an evidence weight of 0.93 (evidence weights are 0.46 and 0.37 for the relative humidity and the temperature effect, respectively). Independently of weather conditions, subadults were on average faster than adults, with an evidence weight of 0.91 for this effect of life-history stage (Table 3, Fig. 5).

Table 3: Averaged model parameters for the individual diffusion coefficients of dispersing *Cornu aspersum* snails. Parameter values are averaged over the complete set of models with shrinkage (see Table S2 in ESM).

	Average effect ± SE	Parameter weight
Subadult	0.42 ± 0.08 *	0.91
Rain	0.27 ± 0.06 *	0.92
Temp.	0.05 ± 0.07	0.37
R.H.	0.02 ± 0.02	0.46
(Intercept)	0.92 ± 2.50	1.00

Parameter weight: the sum of the AIC weights of all models in which the parameter appears. Subadult: effect of the life-history stage being "subadult", compared to adults; Rain: mean daily rainfall; Temp.: mean temperature; R.H.: mean relative humidity. *: average parameter value different from 0, based on 95 % confidence intervals.

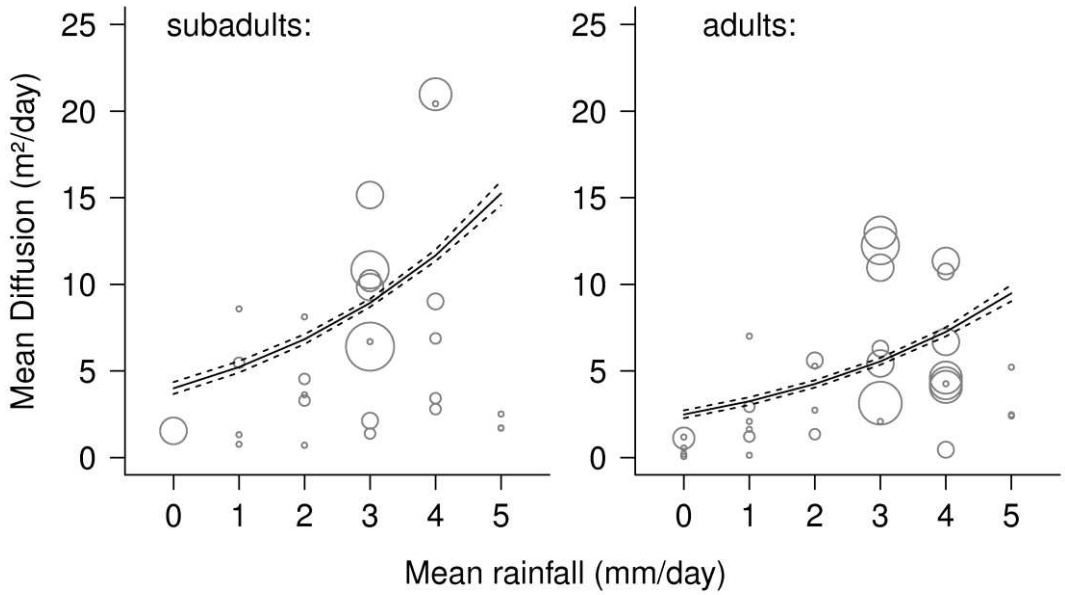

Figure 5: Observed (circles) and predicted (lines) mean diffusion coefficients of dispersing subadults (*n* = 74, left) and adults (*n* = 90, right) of *Cornu aspersum*, as a function of mean daily rainfall during dispersal. For ease of reading, each circle represent the mean observed diffusion coefficient of a group (individuals from the same patch, dispersing *via* the same corridor, see Materials and Methods), for a given mean rainfall level (rounded to the nearest mm). The size of each circle is proportional to the number of individuals. Predictions from the best GLMM (Table 3), based on fixed effects only, are plotted (solid lines) with their 95 % confidence intervals (broken lines).

Discussion

Compared to adults, subadults of the brown garden snail *Cornu aspersum* emigrated more and moved faster and further during transience. Furthermore, we also found that humidity levels and rainfall were the main weather variables affecting both emigration and transience. If the effects of life-history stage and weather (temperature and humidity) on the initiation of dispersal are relatively well-studied (e.g., Tuda and Shima 2002; Bowler and Benton 2009), their effects during the transience phase have been much less investigated (with the exception of wind in flying insects and passively dispersing organisms; e.g., Reynolds et al. 2007). Here, overall effects of life-history stage and weather were similar between emigration and transience. This would indicate the existence of an integrated dispersal strategy, maximizing general dispersal ability (both emigration propensity and dispersal speed) at the life-history stage where benefits of dispersal are maximal (and/or costs minimal).

Weather conditions have a major influence on ectotherms' metabolism and activity; thus, they are usually expected to influence dispersal in similar ways (Delattre 2010). Here, wet weather increased both emigration probability and dispersal speed of land snails. Moreover, in 2012, maximal dispersal distances were close to what is observed in other snails and slugs of similar size (Aubry et al. 2006; Honek and Martinkova 2011), but they were much lower in 2011, which was a dry year. Because land snails and slugs can experience significant water loss through their integument and through mucus secretion, they generally slow down their activity, or even enter a state of dormancy under dry conditions (Cook 2001). The present study logically extends this well-documented weather-dependence of general activity to dispersal movements. However, the average model for the emigration rate also contains a strong humidity × year interaction, with an effect of humidity much stronger in 2012 (Table 2). As humidity ranges in both years did not overlap much (Fig. 3), it is difficult to tell whether this reflects a real difference between years or a non-linear effect of humidity, independent of the year. Prior to release, snails were fed with a composed food. In 2011 only, this resource was added in patches, to compensate for the drought-induced low growth of host plants. *Cornu aspersum* can acquire a strong preference toward a given food resource after conditioning (e.g., Peschel et al. 1996). It is possible that the absence of this familiar food in 2012 rendered the patches less attractive, encouraging emigration. During the 2012 session, wetter conditions also led to an increase in vegetation height and cover in corridors. As a consequence, the contrast between patches and corridors was less marked, compared to 2011. The perception of such contrasts is one of the main proximate mechanisms limiting movement of animals within patches of favourable resources (Haynes and Cronin 2006). When there is no clear boundary between patches and matrix (as in 2012), dispersal can occur as a succession of routine movements (Baguette and Van Dyck 2007). Alternatively, there are indications that high humidity levels have deleterious effects in *C. aspersum* (Klein-Rollais 1993). When maintained at humidity levels above 90 %, snails become unable to regulate correctly their water balance and hyperhydrate. Daily activity rhythms are disturbed, some individuals lose their shell after their columellar muscle break, and

mortality increases to up to 20 times the level observed in optimal conditions (100 % against 4.7 % in 2 months, Klein-Rollais 1993). Thus, it is possible that the observed non-linear response to humidity was independent of the year; in this context, the very high emigration rates observed at high humidity levels could be an emergency response to potentially lethal conditions. Non-linear weather effects and differences in patch quality are both known to influence dispersal (e.g., Delattre 2010 for the former; Mathieu et al. 2010 for the latter). Experiments in strongly contrasted natural or semi-natural landscapes, covering more completely the range of weather conditions experienced by *C. aspersum*, would help to correctly disentangle the respective effects of these environmental conditions in its dispersal.

The existence of a specific dispersing life-history stage, and its nature, depend on the selective pressures on dispersal and/or movement constraints, and how they vary with age or size (Bowler and Benton 2005, 2009). Dispersal is a risky behaviour, entailing many costs (Bonte et al. 2012). When costs are high, larger individuals are expected to be better dispersers (Benard and McCauley 2008). In several mammal species for instance, there is a threshold body mass below which individuals do not disperse (e.g., Debeffe et al. 2012). Based on this and the high energetic cost of movement in land snails (Denny 1980), we hypothesized that adults, which are larger, would be more likely to emigrate and would be faster dispersers than subadults. Indeed, in the invasive slug *Arion lusitanicus*, larger individuals emigrate more and are the fastest dispersers (Honek and Martinkova 2011). Here, the relationship between life-history stage and dispersal in *Cornu aspersum* shows the opposite pattern: subadults are more likely to emigrate and are faster than adults during transience. This is especially surprising for transience: because they have a thinner shell, subadults of *C. aspersum* tend to lose water faster than adults (Klein-Rollais 1993), which would make them more vulnerable to desiccation during prolonged movement. This suggests direct costs of locomotion are not the main driving force acting on dispersal. Indeed, the fastest observed snails dispersed 10 m in 2 days or less, and 45 m in up to 23 days, which is only about half the speed of some walking insects (e.g., Schooley and Wiens

2004), when energetic costs of movement are theoretically much higher (Denny 1980). Altogether, this hints at the existence of other, non-energy related, stage- or size-dependent benefits and costs of dispersal.

Negative size-dependent dispersal, where smaller individuals disperse more, has been associated with intraspecific competition (Bowler and Benton 2005). When the cost of competition is higher than the cost of dispersal, inferior competitors are expected to be more prone to emigrate. This could be the case in *Cornu aspersum*, as subadults do suffer from interference competition when placed with adults (Dan and Bailey 1982). Intraspecific competition can also affect dispersal distances. When the cost of moving further is lower than the cost of settling in, or close to, a highly competitive patch, actively dispersing animals should pass over this patch and continue to disperse, as recently demonstrated in the two-spotted mite (Bitume et al. 2013). In this context, less competitive individuals would move further, as observed in our setup. However, we did not observe an effect of density on dispersal in 2011 (see Material and Methods), which would be expected if dispersal was driven by intraspecific competition. It should be noted that the initial densities we used were in the higher range of natural population densities, and closer to those observed in extensive snail farms (Dan 1978; González et al. 2008). Using densities closer to those observed in natural populations should help to evaluate this possible effect of competition on dispersal rates and dispersal distances.

Dispersal prior to sexual maturation can also be selected as a means to avoid inbreeding, especially when individuals are unable to recognize kin (Bowler and Benton 2005). Helicid snails seem unable to discriminate between siblings and non-siblings when it comes to mate choices (Baur and Baur 1997) or egg cannibalism (Baur 1990). In this context, avoiding matings between relatives is likely to be one of the main drivers of subadult dispersal in *C. aspersum*, which is moreover a species extremely sensitive to the deleterious effects of inbreeding (Albuquerque de Matos and Serra 1984). Thus, subadult dispersal in the brown garden snail could be seen, as in many other groups, as a case of natal dispersal, i.e., the movement from the

site of birth to the site of first reproduction (Clobert et al. 2012). However, interpreting the subadult dispersal patterns observed here as natal dispersal *stricto sensu* is difficult for at least two reasons. First, pre-capture dispersal and reproductive histories of the individuals tested here are unknown. Then, in helicid land snails, subadults are able to mate, produce sperm and lay eggs, albeit with less success than adults (Fearnley 1993; Kupfernagel and Baur 2011), making it difficult to equal subadult/adult with pre-breeding/post-breeding. Laboratory experiments, where the age and the reproductive history of individuals can be known easily, are needed to determine whether subadult dispersal in *C. aspersum* really corresponds to natal dispersal. Tomiyama and Nakane (1993) proposed an alternative hypothesis to explain similar dispersal patterns in the giant snail *Achatina fulica*. *Achatina fulica* is one of the few animal species known to present a protandric simultaneous hermaphroditism, i.e., a mixed sex allocation pattern in which individuals mature and reproduce initially as males, and later become functional simultaneous hermaphrodites (Baeza 2007). Male subadults can mate with many snails without having to pay the cost of egg creation, when adults must pay these costs, and thus have less energy to invest in movement. In these conditions, according to Tomiyama and Nakane (1993), natural selection should favour high dispersal and multiple matings in male subadults, and sedentarity in fully hermaphroditic adults. This hypothesis focuses on the energetic costs of reproduction, but such a dispersal strategy would also lead to reduced inbreeding by scattering related snails before their full sexual maturity. This has yet to be fully tested, but there is indication that *C. aspersum* might be a protandric simultaneous hermaphroditic species, with subadults being functionally male (Bride and Gomot 1991; Fearnley 1993).

Dispersal is a complex process, under multiple, simultaneous and sometimes contradictory selective pressures (Clobert et al. 2012). Thus, it is possible, and even likely, that the three mechanisms proposed here (namely competition avoidance, natal dispersal linked to inbreeding avoidance and differences in costs between “males” and hermaphrodites if there is protandric

simultaneous hermaphroditism), simultaneously influence, to varying degrees, *C. aspersum* dispersal. Their relative importance could have profound impacts on metapopulation dynamics and the persistence of local populations. For instance, if subadult dispersal is mainly linked to mate search, as in Tomiyama and Nakane's (1993) hypothesis, immigration should be higher in high-density patches. This would increase the extinction risk of small populations, as dispersers settle in already large populations and empty patches are not recolonized (Sæther et al. 1999). On the other hand, when dispersal is mainly a response to competition, dispersers tend to settle more in low-density patches, increasing the local growth rate and decreasing the local extinction risk (demographic rescue effect; Sæther et al. 1999; Hanski 2012). Moreover, dispersal before reproductive maturity and the arrival of unrelated individuals would decrease inbreeding depression and its deleterious effects, especially in low-density patches (genetic rescue effect; Saccheri and Brakefield 2002; Hanski 2012). In order to better understand the relative importance of these mechanisms, the effect of inter-individual variation in size, age and reproductive development on all steps of dispersal (including immigration) should be investigated. Overall, our results highlight the necessity of studying more diverse reproductive systems regarding dispersal, as a similar pattern might be caused by different underlying strategies in hermaphrodites than in gonochoric animals. Such "alternative" dispersal strategies could have many interesting, yet unstudied, consequences in terms of life-history evolution, sexual selection and population dynamics.

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References

Albuquerque de Matos RM, Serra JA (1984) Taxonomic polymorphism and intrinsic factors in *Helix aspersa*. Brotéria-Genética 5:181–220

Aubry S, Labaune C, Magnin F, Roche P, Kiss L (2006) Active and passive dispersal of an invading land snail in Mediterranean France. J Anim Ecol 75:802–813

Baeza JA (2007) Male mating opportunities affect sex allocation in a protandric-simultaneous hermaphroditic shrimp. Behav Ecol Sociobiol 61:365–370

Baguette M, Van Dyck H (2007) Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. Landscape Ecol 22:1117–1129

Bailey SER (1975) The seasonal and daily patterns of locomotor activity in the snail *Helix aspersa* Müller, and their relation to environmental variables. J Mollus Stud 41:415–428

Bailey SER (1989) Daily cycles of feeding and locomotion in *Helix aspersa*. Haliotis 19:23–31.

Barker GM (2001a) The biology of terrestrial molluscs. CABI Publishing, Wallingford

Barker GM (2001b) Gastropods on land: phylogeny, diversity and adaptive morphology. In: Barker GM (ed) The biology of terrestrial molluscs. CABI Publishing, Wallingford, pp 1–146

Barker GM (2002) Molluscs as crop pests. CABI Publishing, Wallingford

Barker GM (2004) Natural enemies of terrestrial molluscs. CABI Publishing, Wallingford

Bartoń KA (2012) R package MuMIn : model selection and model averaging based on information criteria (AIC_c and alike). http://mumin.r-forge.r-project.org/

Bates D, Maechler M, Bolker B (2011) R package lme4: linear mixed-effects models using S4 classes. http://lme4.r-forge.r-project.org/

Baur B (1990) Egg cannibalism in hatchlings of the land snail *Helix pomatia*: nutritional advantage may outweigh lack of kin recognition. Malacol Rev 23:103–105

Baur A (1993a) Effects of food availability and intraspecific and interspecific interactions on the dispersal tendency in the land snail *Chondrina clienta*. J Zool 230:87–100

Baur B (1993b) Population structure, density, dispersal and neighbourhood size in *Arianta arbustorum*. Ann Naturhist Mus Wien 94/95:307–321

Baur B, Baur A (1997) Random mating with respect to relatedness in the simultaneously hermaphroditic land snail *Arianta arbustorum*. Invertebr Biol 116:294

Benard MF, McCauley SJ (2008) Integrating across life-history stages: consequences of natal habitat effects on dispersal. Am Nat 171:553–567

Bitume EV, Bonte D, Ronce O, Bach F, Flaven E, Olivieri I, Nieberding CM (2013) Density and genetic relatedness increase dispersal distance in a subsocial organism. Ecol Lett 16:430–437

Bonte D, Van Dyck H, Bullock JM, Coulon A, Delgado M, Gibbs M, Lehouck V, Matthysen E, Mustin K, Saastamoinen M, Schtickzelle N, Stevens VM, Vandewoestijne S, Baguette M, Barton K, Benton TG, Chaput-Bardy A, Clobert J, Dytham C, Hovestadt T, Meier CM, Palmer SCF, Turlure C, Travis JMJ (2012) Costs of dispersal. Biol Rev 87:290–312

Bowler DE, Benton TG (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biol Rev 80:205–225

Bowler DE, Benton TG (2009) Variation in dispersal mortality and dispersal propensity among individuals: the effects of age, sex and resource availability. J Anim Ecol 78:1234–1241

Bride J, Gomot L (1991) Asynchronisme du développement du tractus génital de l'escargot *Helix aspersa* pendant la croissance et la reproduction. Reprod Nut Dev 31:81–96 (in French with English abstract)

Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information-theoretic approach, 2nd edn. Springer, New York

Clobert J, Baguette M, Benton TG, Bullock JM (2012) Dispersal ecology and evolution. Oxford University Press, Oxford

Cook A (2001) Behavioural ecology: on doing the right thing, in the right place at the right time. In: Barker GM (ed) The biology of terrestrial molluscs. CABI Publishing, Wallingford, pp 447–488

Costello CM, Creel SR, Kalinowski ST, Vu NV, Quigley HB (2008) Sex-biased natal dispersal and inbreeding avoidance in American black bears as revealed by spatial genetic analyses. Mol Ecol 17:4713–4723

Cowie RH (2011) Snails and slugs. In: Simberloff D, Rejmanek M (eds) Encyclopedia of Biological Invasions. University of California Press, Berkeley, pp 634–643

Dale S (2001) Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. Oikos 92:344–356

Dan N (1978) Studies on the growth and ecology of *Helix aspersa* Müller. PhD thesis, University of Manchester, Manchester

Dan N, Bailey SER (1982) Growth, mortality, and feeding rates of the snail *Helix aspersa* at different population densities in the laboratory, and the depression of activity of helicid snails by other individuals, or their mucus. J Mollus Stud 48:257–265.

Danchin E, Cam E (2002) Can non-breeding be a cost of breeding dispersal? Behav Ecol 51:153–163

Debeffe L, Morellet N, Cargnelutti B, Lourtet B, Bon R, Gaillard JM, Mark Hewison AJ (2012) Condition-dependent natal dispersal in a large herbivore: heavier animals show a greater propensity to disperse and travel further. J Anim Ecol 81:1327–1337

Delattre T (2010) Influence de la structure du paysage et des conditions météorologiques sur le comportement de dispersion de *Maniola jurtina* (Lepidoptera : Nymphalidae, L.) dans un agroécosystème bocager. PhD thesis, Université de Rennes 1 / Université Européenne de Bretagne, Rennes (In French with chapters in English)

Denny M (1980) Locomotion: the cost of gastropod crawling. Science 208:1288–1290

Dörge N, Walther C, Beinlich B, Plachter H (1999) The significance of passive transport for dispersal in terrestrial snails (Gastropoda, Pulmonata). Z Ökologie u Naturschutz 8:1–10.

Fearnley RH (1993) Sexual selection, dispersal and reproductive behaviour in hermaphrodite land snails, with particular reference to *Helix aspersa* Müller (Pulmonata: Gastropoda). PhD thesis, University of Manchester, Manchester

González O, Pérez Camargo G, Membiela M, Frezza D, Bartoloni N, Vieites C (2008) Effect of population density on snail productivity (*Helix aspersa*) in an open sky system fed with Swiss chard and a balanced food supplement. Cien Inv Agr 35:251–257

Guerra PA (2011) Evaluating the life-history trade-off between dispersal capability and reproduction in wing dimorphic insects: a meta-analysis. Biol Rev 86:813–835

Guiller A, Martin M-C, Hiraux C, Madec L (2012) Tracing the invasion of the mediterranean land snail *Cornu aspersum aspersum* becoming an agricultural and garden pest in areas recently introduced. PLoS ONE 7:e49674

Hanski I (2012) Dispersal and eco-evolutionary dynamics in the Glanville fritillary butterfly. In: Clobert J, Baguette M, Benton TG, Bullock JM (eds) Dispersal ecology and evolution. Oxford University Press, UK, pp 290–303

Haynes KJ, Cronin JT (2006) Interpatch movement and edge effects: the role of behavioral responses to the landscape matrix. Oikos 113:43–54

Henry P-Y, Jarne P (2007) Marking hard-shelled gastropods: tag loss, impact on life-history traits, and perspectives in biology. Invertebr Biol 126:138–153

Honek A, Martinkova Z (2011) Body size and the colonisation of cereal crops by the invasive slug *Arion lusitanicus*. Ann Appl Biol 158:79–86

Iglesias J, Castillejo J (1999) Field observations on feeding of the land snail *Helix aspersa* Müller. J Mollus Stud 65:411 –423

Ims RA, Hjermann DØ (2001) Condition-dependent dispersal. In: Clobert J, Danchin E, Dhondt A, Nichols J (eds) Dispersal. Oxford University Press, Oxford, pp 203–216

Klein-Rollais D (1993) Contribution à l'étude de la balance hydrique et de sa régulation chez l'escargot Petit-Gris, *Helix aspersa* Müller (Mollusque Gastéropode Pulmoné). PhD thesis, Université de Rennes 1, Rennes (in French)

Kupfernagel S, Baur B (2011) Sperm utilization in subadult and adult simultaneous hermaphrodite snails mating in the wild. Can J Zool 89:1041–1049

Mathieu J, Barot S, Blouin M, Caro G, Decaëns T, Dubs F, Dupont L, Jouquet P, Nai P (2010) Habitat quality, conspecific density, and habitat pre-use affect the dispersal behaviour of two earthworm species, *Aporrectodea icterica* and *Dendrobaena veneta*, in a mesocosm experiment. Soil Biol Biochem 42:203–209

Miller TEX, Inouye BD (2013) Sex and stochasticity affect range expansion of experimental invasions. Ecology Letters 16:354–361

Oosterhoff LM (1977) Variation in growth rate as an ecological factor in the landsnail *Cepaea nemoralis* (l.). Neth J Zool 27:1–132.

Perrin N, Goudet J (2001) Inbreeding, kinship, and the evolution of natal dispersal. In: Clobert J, Danchin E, Dhondt A, Nichols J (eds) Dispersal. Oxford University Press, Oxford, pp 123–142

Peschel M, Straub V, Teyke T (1996) Consequences of food-attraction conditioning in *Helix*: a behavioral and electrophysiological study. J Comp Physiol A 178:317–327

R Development Core Team (2011) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org

Reynolds AM, Bohan DA, Bell JR (2007) Ballooning dispersal in arthropod taxa: conditions at take-off. Biol Lett 3:237 –240

Ronce O (2007) How does it feel to be like a rolling stone? Ten questions about dispersal evolution. Annu Rev Ecol Evol Syst 38:231–253

Saccheri IJ, Brakefield PM (2002) Rapid spread of immigrant genomes into inbred populations. Proc R Soc Lond B 269:1073–1078

Sæther B-E, Engen S, Lande R (1999) Finite metapopulation models with density–dependent migration and stochastic local dynamics. Proc R Soc Lond B 266:113–118

Schooley RL, Wiens JA (2004) Movements of cactus bugs: Patch transfers, matrix resistance, and edge permeability. Landscape Ecol 19:801–810

Starrfelt J, Kokko H (2012) The theory of dispersal under multiple influences. In: Clobert J, Baguette M, Benton TG, Bullock JM (eds) Dispersal ecology and evolution. Oxford University Press, Oxford, pp 19–28

Stratton LW (1964) The non-marine Mollusca of the Parish of Dale. Field Studies 2:41–52.

Tomiyama K, Nakane M (1993) Dispersal patterns of the giant African snail, *Achatina fulica* (Férussac) (Stylommatophora: Achatinidae), equipped with a radio-transmitter. J Mollus Stud 59:315 –322

Tuda M, Shima K (2002) Relative importance of weather and density dependence on the dispersal and on-plant activity of the predator *Orius minutus*. Popul Ecol 44:0251–0257

Turchin P (1998) Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Sunderland

Electronic supplementary material

Dahirel M · Ansart A · Madec L. **Stage- and weather-dependent dispersal in the brown garden snail *Cornu aspersum*.** *Population Ecology.*

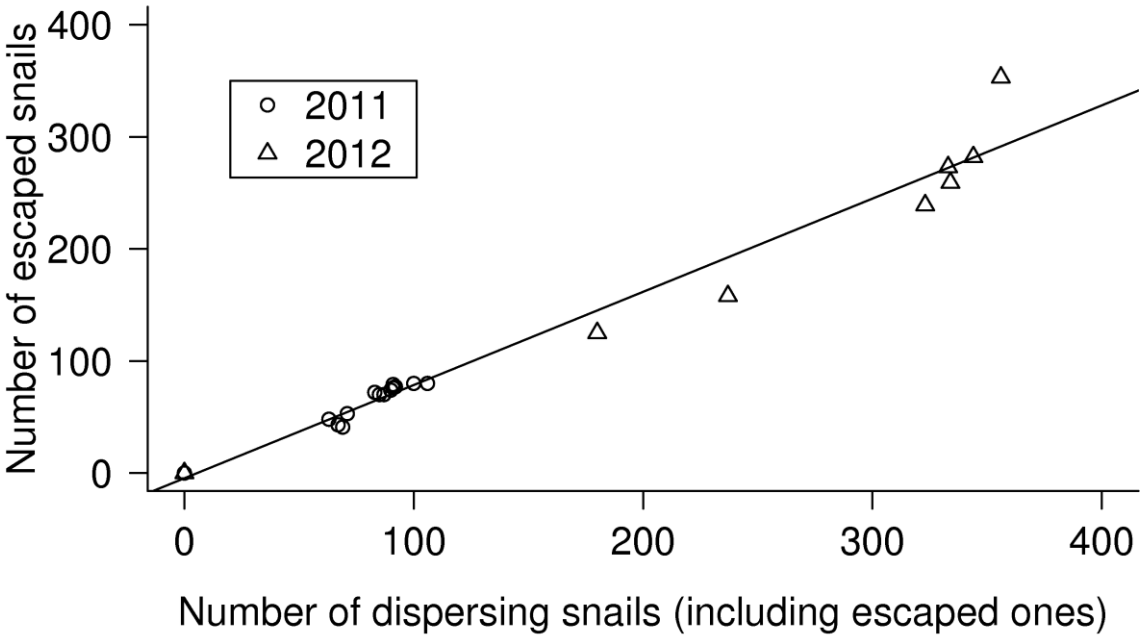

Figure S1: Relationship between the number of dispersing individuals and the number of escaped individuals. Each point corresponds to a recapture occasion. Individuals are considered escaped on a given recapture occasion if they were not found in subsequent recapture sessions; dispersing snails are individuals found outside the circle of radius 1.2 m centred on their release point (see Materials and Methods), plus the escaped snails. The equation for the linear regression is $y = 0.811x$, $R^2 = 0.98$.

Table S1: Set of models for the emigration probability between successive recaptures. Models are GLMMs with binomial errors and logit links, ranked by increasing AIC. Only the first 50 models, cumulating 99.5 % of AIC weights, are presented. (Int.): Intercept; R.H.: mean relative humidity; Duration: time between successive recaptures; Rain: mean daily rainfall; Subad.: effect of the life-history stage being "subadult", compared to adults ; Temp.: mean temperature; *df*: degrees of freedom; logLik: maximized log-likelihood; w_i: Akaike weights; cum(w_i) : cumulated Akaike weights. Interactions between the year effect and other variables are denoted by a "×" sign.

(Int.)	R.H.	Duration	Rain	Subad.	Year	Year × R.H.	Year × Rain	Temp.	Year × Duration	Year × Subadult	Year × Temp.	*df*	logLik	AIC	ΔAIC	w_i	cum(w_i)
-17.21	0.20	0.04	0.00	0.15	-24.25	0.33	-0.20					9	-160.20	339.38	0.00	0.10	0.10
-17.39	0.21	0.04	-0.09	0.15	-19.39	0.27						8	-161.59	339.97	0.59	0.08	0.18
-13.73	0.18	0.04	0.05	0.15	-27.33	0.37	-0.26	-0.10				10	-159.39	339.99	0.60	0.08	0.26
-17.10	0.20	0.04		0.16	-16.67	0.23						7	-162.77	340.14	0.76	0.07	0.33
-17.75	0.21	0.04	0.00	0.15	-28.75	0.39	-0.21		-0.02			10	-159.64	340.50	1.11	0.06	0.39
-14.59	0.18	0.04		0.16	-18.20	0.25		-0.07				8	-162.12	341.02	1.64	0.05	0.44
-17.98	0.21	0.04	-0.09	0.15	-21.98	0.30			-0.02			9	-161.07	341.12	1.74	0.04	0.48
-17.74	0.21	0.04		0.16	-18.85	0.26			-0.01			8	-162.20	341.19	1.80	0.04	0.52
-17.21	0.20	0.04	0.00	0.15	-24.27	0.33	-0.20			0.02		10	-160.19	341.60	2.22	0.03	0.56
-15.78	0.20	0.04	-0.07	0.15	-19.96	0.28		-0.05				9	-161.37	341.74	2.35	0.03	0.59
-14.75	0.19	0.04	0.04	0.15	-29.91	0.41	-0.26	-0.08	-0.01			11	-159.19	341.85	2.47	0.03	0.62

Table S1 (continued)

(Int.)	R.H.	Duration	Rain	Subad.	Year	Year × R.H.	Year × Rain	Temp.	Year × Duration	Year × Subadult	Year × Temp.	*df*	logLik	AIC	ΔAIC	w_i	cum(w_i)
-17.39	0.21	0.04	-0.09	0.15	-19.41	0.27				0.02		9	-161.59	342.16	2.78	0.03	0.64
-13.73	0.18	0.04	0.05	0.15	-27.34	0.37	-0.26	-0.10		0.01		11	-159.38	342.23	2.84	0.03	0.67
-13.63	0.18	0.04	0.05	0.15	-27.49	0.37	-0.26	-0.10			0.01	11	-159.38	342.23	2.85	0.03	0.70
-17.10	0.20	0.04		0.15	-16.69	0.23				0.02		8	-162.76	342.30	2.92	0.02	0.72
-17.74	0.21	0.04	0.00	0.15	-28.76	0.39	-0.21		-0.02	0.01		11	-159.64	342.74	3.35	0.02	0.74
-15.67	0.20	0.04		0.16	-19.32	0.27		-0.06	-0.01			9	-161.90	342.78	3.40	0.02	0.76
-14.59	0.18	0.04		0.15	-18.21	0.25		-0.07		0.02		9	-162.11	343.21	3.83	0.02	0.77
-14.58	0.18	0.04		0.16	-18.20	0.25		-0.07			0.00	9	-162.12	343.22	3.84	0.02	0.79
-17.19	0.21	0.04	-0.08	0.15	-21.92	0.30		-0.02	-0.01			10	-161.03	343.28	3.89	0.01	0.80
-17.98	0.21	0.04	-0.09	0.15	-21.99	0.30			-0.02	0.02		10	-161.06	343.34	3.95	0.01	0.82
-17.73	0.21	0.04		0.15	-18.87	0.26			-0.01	0.02		9	-162.19	343.38	3.99	0.01	0.83
-14.07	0.18	0.04	0.05	0.15	-36.55	0.44	-0.25	-0.10	-0.03		0.27	12	-158.86	343.47	4.09	0.01	0.85
-15.02	0.19	0.04		0.16	-29.35	0.33		-0.07	-0.04		0.34	10	-161.34	343.89	4.50	0.01	0.86
-16.15	0.20	0.04	-0.08	0.15	-19.28	0.27		-0.04			-0.04	10	-161.35	343.92	4.54	0.01	0.87
-15.77	0.20	0.04	-0.07	0.15	-19.97	0.28		-0.05		0.02		10	-161.37	343.95	4.57	0.01	0.88

Table S1 (continued)

(Int.)	R.H.	Duration	Rain	Subad.	Year	Year × R.H.	Year × Rain	Temp.	Year × Duration	Year × Subadult	Year × Temp.	*df*	logLik	AIC	ΔAIC	w_i	cum(w_i)
-17.12	0.20	0.04	0.00		-24.24	0.33	-0.20					8	-163.64	344.06	4.68	0.01	0.89
-14.75	0.19	0.04	0.04	0.15	-29.92	0.41	-0.26	-0.08	-0.01	0.01		12	-159.19	344.12	4.73	0.01	0.90
-13.63	0.18	0.04	0.05	0.15	-27.50	0.37	-0.26	-0.10		0.01	0.01	12	-159.38	344.50	5.12	0.01	0.91
-13.64	0.18	0.04	0.05		-27.32	0.37	-0.26	-0.10				9	-162.82	344.64	5.25	0.01	0.91
-17.30	0.21	0.04	-0.09		-19.38	0.27						7	-165.03	344.68	5.29	0.01	0.92
-16.48	0.20	0.04	-0.07	0.15	-29.71	0.35		-0.04	-0.03		0.28	11	-160.66	344.80	5.41	0.01	0.93
-17.01	0.20	0.04			-16.65	0.23						6	-166.21	344.88	5.49	0.01	0.93
-15.67	0.20	0.04		0.15	-19.33	0.27		-0.06	-0.01	0.02		10	-161.89	345.00	5.61	0.01	0.94
-17.66	0.21	0.04	0.00		-28.74	0.39	-0.21		-0.02			9	-163.08	345.15	5.77	0.01	0.95
-14.58	0.18	0.04		0.15	-18.22	0.25		-0.07		0.02	0.00	10	-162.11	345.44	6.05	0.01	0.95
-17.19	0.21	0.04	-0.08	0.15	-21.93	0.30		-0.02	-0.01	0.02		11	-161.02	345.51	6.13	0.00	0.96
-14.50	0.18	0.04			-18.18	0.25		-0.07				7	-165.56	345.73	6.35	0.00	0.96
-14.06	0.18	0.04	0.05	0.15	-36.56	0.44	-0.25	-0.10	-0.03	0.01	0.27	13	-158.86	345.76	6.38	0.00	0.96
-17.89	0.21	0.04	-0.09		-21.96	0.30			-0.02			8	-164.51	345.81	6.42	0.00	0.97

Table S1 (end)

(Int.)	R.H.	Duration	Rain	Subad.	Year	Year × R.H.	Year × Rain	Temp.	Year × Duration	Year × Subadult	Year × Temp.	*df*	logLik	AIC	ΔAIC	w_i	cum(w_i)
-17.65	0.21	0.04			-18.83	0.26			-0.01			7	-165.65	345.90	6.52	0.00	0.97
-15.02	0.19	0.04		0.15	-29.37	0.33		-0.07	-0.04	0.02	0.34	11	-161.33	346.13	6.74	0.00	0.98
-16.15	0.20	0.04	-0.08	0.15	-19.29	0.27		-0.04		0.02	-0.04	11	-161.35	346.16	6.78	0.00	0.98
-15.69	0.19	0.04	-0.07		-19.95	0.28		-0.05				8	-164.82	346.42	7.04	0.00	0.98
-14.66	0.19	0.04	0.04		-29.90	0.41	-0.26	-0.08	-0.01			10	-162.63	346.48	7.09	0.00	0.99
-13.54	0.18	0.04	0.05		-27.48	0.37	-0.26	-0.10			0.01	10	-162.82	346.86	7.48	0.00	0.99
-16.48	0.20	0.04	-0.07	0.15	-29.72	0.35		-0.04	-0.03	0.02	0.28	12	-160.66	347.06	7.68	0.00	0.99
-15.58	0.20	0.04			-19.30	0.27		-0.06	-0.01			8	-165.34	347.47	8.09	0.00	0.99
-14.49	0.18	0.04			-18.18	0.25		-0.07			0.00	8	-165.56	347.91	8.53	0.00	0.99

Table S2: Set of models for the individual diffusion coefficients of dispersing snails. Models are GLMMs with Gaussian errors and log links, ranked by increasing AIC. (Int.): Intercept; Subad.: effect of the life-history stage being "subadult", compared to adults; Rain: mean daily rainfall; R.H.: mean relative humidity, Temp.: mean temperature; *df*: degrees of freedom; logLik: maximized log-likelihood; w_i : Akaike weights; cum(w_i) : cumulated Akaike weights.

(Int.)	Subad.	Rain	R.H.	Temp.	*df*	logLik	AIC	ΔAIC	w_i	cum(w_i)
0.91	0.48	0.27			5	-601.27	1212.53	0.00	0.31	0.31
-2.19	0.44	0.22	0.04		6	-600.61	1213.22	0.69	0.22	0.53
-1.75	0.47	0.35		0.15	6	-600.74	1213.48	0.95	0.19	0.72
-4.84	0.44	0.31	0.04	0.13	7	-600.15	1214.29	1.76	0.13	0.85
-3.57	0.36		0.07		5	-603.35	1216.71	4.18	0.04	0.89
-2.74		0.17	0.05		5	-603.81	1217.61	5.08	0.02	0.92
1.25		0.24			4	-605.02	1218.04	5.50	0.02	0.94
-2.78	0.37		0.06	-0.04	6	-603.22	1218.43	5.90	0.02	0.95
-5.53		0.26	0.06	0.13	6	-603.35	1218.70	6.17	0.01	0.97
-3.68			0.07		4	-605.48	1218.95	6.42	0.01	0.98
-1.33		0.32		0.15	5	-604.52	1219.04	6.50	0.01	0.99
-3.22			0.07	-0.02	5	-605.44	1220.87	8.34	0.00	1.00
1.76	0.42				4	-607.04	1222.07	9.54	0.00	1.00
1.97					3	-609.58	1225.17	12.63	0.00	1.00
3.32	0.44			-0.13	5	-611.53	1233.06	20.53	0.00	1.00
2.94				-0.10	4	-615.58	1239.17	26.63	0.00	1.00